DESCRIPTIONS OF NEW AFRICAN EARTHWORMS, INCLUDING A NEW GENUS OF MONILIGASTRIDAE.

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The United States National Museum has a small collection of earthworms made near Lamu on the eastern coast of British East Africa. The collection was made by William Astor Chanler in 1892; and, besides several fragmentary specimens, contains seven worms sufficiently complete for identification.

These specimens though few in number are of much interest. Two new species of *Polytoreutus* are represented, one by five individuals and another by a single specimen. The remaining specimen represents a new genus of the family Moniligastridae. This is the first known occurrence of this family in Africa; and, of still greater interest, the new form has anatomical relations which ally it quite closely with the Haplotaxid genus *Pelodrilus* and with the Megascolecid genus *Acanthodrilus*. It may reasonably be considered as a modern representative of a very early, primitive type of earthworms.

This paper forms No. 126 of the series of contributions from the zoological laboratory of the University of Illinois.

Family MONILIGASTRIDAE.

Setae, simple pointed, sigmoid, four pair per somite. Clitellum on three to six somites, including those bearing genital pores. Spermiducal pores, one or two pair; in or near 10/11, 11/12, or 12/13. Oviducal pores, one pair; in 11/12 or on 13 or 14. Spermathecal pores, one or two pair in 7/8 or 8/9 or 7/8 and 8/9. Esophagus with two gizzards anterior to 10 or two to ten gizzards at beginning of intestine. Last "hearts," two somites anterior to ovarian somite. Meganephric. Spermaries and spermiducal funnels, one or two pair; included in one or two pair of sperm vesicles. Sperm ducts open into prostate glands or independently of them. Ovaries, one pair. Ovisacs, one pair; extend posteriorly from posterior septum of ovarian somite. Spermathecae, one or two pair; with long tubular spermathecal ducts.

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SYNGENODRILUS, new genus.

Prostate gland pores, distinct from spermiducal pores; in close proximity to ventral pairs of setae. Spermiducal pores, one pair; anterior to oviducal pores. Oviducal pores on 14. Gizzards anterior to 10. Posterior "hearts" in 11. Meganephric. Spermaries and spermiducal funnels, enclosed in sperm vesicles. Prostate glands, not connected with sperm ducts. Ovaries in 13. Ovisacs extend posteriorly from 13 through several somites. Spermathecae, without diverticula or appendages.

Genotype.—Syngenodrilus lamuensis, new species.

SYNGENODRILUS LAMUENSIS, new species.

Length, 5.2 cm. Diameter (maximum), 0.4 cm. Somites, 137. Clitellum, 11–16; cingulum. Genital papillae, none obvious. Setae, very small; $aa:ab:bc:cd=17:1:17:\frac{10}{11}$; $dd=\frac{9}{14}$ circumference. Nephridiopores, first on 4; at anterior margin of somite; some midway between seta line *cd* and mid-dorsal line, others in seta line *cd*. Spermiducal pores, inconspicuous; at anterior margin of 13; slightly ventrad of seta line *cd*. Prostate gland pores, 11, 12, and 13, slightly dorsad of seta line *b*. Oviducal pores, on 14, slightly anteriad and dorsad of *b*. Spermathecal pores, paired in 7/8 and 8/9; slightly ventrad of seta line *cd*. Septa 5/6–7/8, very strongly thickened; septa 8/9–12/13, very thin and somewhat displaced and imperfectly developed. Two gizzards in 8 and 9. Hearts, 6–11. Nephridia, paired; lacking in 1–3 and 11–12. Paired spermaries and spermiducal funnels, inclosed in paired sperm vesicles in 10 and 11. Sperm ducts of each side, much contorted and unite into a single duct, which is without penial or atrial modification. Prostate glands, small; one pair each in 11, 12, and 13. Sperm sacs, one pair included within ovisacs and extend posteriorly to 20. Ovaries, extensive; in 13. Oviducal funnels and ducts, broad and short. Spermathecae, simple; long and slender; paired in 8 and 9.

One specimen, collected at Mkonumbi near Lamu, British East Africa, by William Astor Chanler in 1892.

Holotype.—Cat. No. 16833, U.S.N.M.

The specimen in alcohol is apparently considerably contracted and without obvious color differentiation. Sagittal sections were made from one half of the anterior 22 somites, the other half being left united with the remainder of the worm. The alimentary tract had of course not been freed from dirt before preservation and the clitellar hypodermis proved to be rather difficult to section; and hence the series of sections is defective in some respects, although on the whole it is very good and has made possible the determination of some facts in the anatomy which could not otherwise have been obtained.

External characters.—There is nothing to indicate that the worm is not complete and that the length, 5.2 cm. and the number of somites, 137, are not normal for the species. The maximum diameter, 0.4 cm., is reached in somites 8–14; while anterior to 8 the diameter decreases quite uniformly to the first somite, where it is about 0.15 cm.; posterior to 14, the decrease is very gradual to 0.35 cm. near the posterior end; the trunk being nearly cylindrical throughout. The prostomium is scarcely recognizable and presumably is prolobic. The somites posterior to 15 are each of about one-half the length of the more anterior ones, which are nearly uniform, except that 1–3 are slightly shorter and 15 is about two-thirds as long as 14. Intersegmental grooves are distinct and posterior to 16 each somite has a median ridge on which the setae are borne and which is bounded anteriorly by a distinct annular groove just in front of the setae. The anterior somites are without such annular grooves.

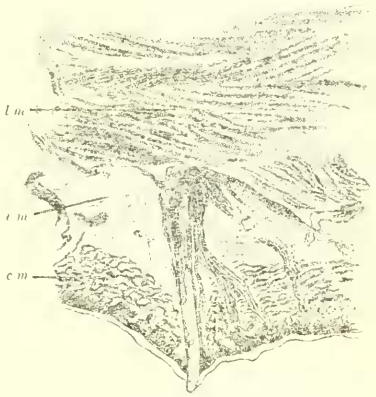

FIG. 1.—SYNGENODRILUS LAMUENSIS. SETA *b* OF SOMITE 7. ×175. *c m*, CIRCULAR MUSCULAR LAYER; *i m*, INTERMUSCULAR LAYER; *l m*, LONGITUDINAL MUSCULAR LAYER.

The clitellum is most obvious on 11–14, where the intersegmental grooves are less distinct, but also includes 15 and 16, which have a similar glandular, thickened hypodermis, but are more sharply set off by intersegmental grooves and are somewhat shorter. The clitellum is developed on the ventral as well as on the dorsal surface and is but one cell thick, as in other Moniligastridae. No genital papillae are obvious, although the worm is apparently at the height of sexual activity.

The setae (figs. 1 and 2) are very small, very closely paired, and no sculpture nor differentiation into special forms as sexual setae has been observed. Posterior to the clitellum, $aa:ab:bc:cd=17:1:17:\frac{10}{11}$. *dd* is about $\frac{9}{14}$ of the circumference. These numbers are from averages of several measurements. Length of setae, 0.14–0.19 mm.

The nephridiopores are near the anterior margin of the somites, and the most anterior one found is on the fourth somite. None were found on 10, 11, 12, and 14. Those of 4–9, 13, and 16 are about halfway from seta line *cd.* to the mid-dorsal line, while those of 15 and 17–22 are in the line *cd.* They are obvious only in sections, and hence their position is not known posterior to 22.

There is but one pair of spermiducal pores, and they are recognizable only in sections. They are very close to the anterior border of 13 and somewhat ventrad of seta line *cd.* Three prostate gland pores

are present in the sectioned half of the worm and are slightly dorsad of *b* in 11, 12, and 13. Corresponding pores are doubtless present on the unsectioned half of the worm, although they are not recognizable because of their small size. The oviducal pores are on 14 and are a little anterior to and slightly dorsad of *b*. The spermathecal pores are paired in 7/8 and 8/9 and are slightly ventrad of seta line *cd*.

Internal characters.—The structure of the body wall differs from that more commonly found in earthworms. The circular and longitudinal muscle layers are separated by an intervening layer of tissue of an entirely different nature (figs. 1 and 4). It is not stained by the hematoxylin or eosin used, and hence in the sections is sharply differentiated in color as well as in structure. The thickness of the layer is about equivalent to that of the layer of circular muscle fibers. In section it has a very distinctly laminated appearance, there being more commonly four to six laminae, which become much reduced in thickness opposite the intersegmental grooves. Similar conditions are found in sections of a specimen of *Drawida bournei* Michaelsen, for which we are indebted to Doctor Michaelsen, and which is the only material of the family available for comparison. A detailed histological study of this tissue has not yet been attempted by us, but there is no indication of its being fibrous, as the transverse and longitudinal sections present much the same appearance.

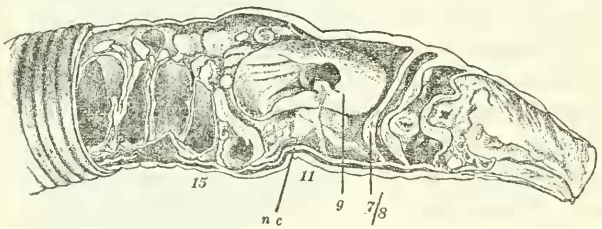

FIG. 2.—SYNGENODRILUS LAMUENSIS. ANTERIOR END FROM WHICH PIECE WAS REMOVED FOR SECTIONING. ×5. *g*, GIZZARD; *n c*, NERVE CORD; 7/8, SEPTUM BETWEEN 7 AND 8.

Septa 5/6–7/8 (fig. 2) are very strongly thickened and the ones posterior to 7/8 are extremely thin and delicate. Those between 7/8 and 13/14 are so extensively displaced and obscure that the exact determination of the internal boundaries of the somites and the assignment of the contained organs to their proper somites is rendered somewhat difficult. What is assumed to be septum 8/9 joins the dorsal wall at 10/11 and the ventral wall at the middle of 10, as indicated by the external metamerism and the setae. Septum 13/14 is attached to the body a little way posterior to 13/14, as indicated by the intersegmental groove. Between septa 8/9 and 13/14 there seem to be but two septal layers connecting with the body wall, although there are evidences of more septa among the organs. The anterior one of these two layers is perhaps the combined septa 9/10, 10/11, and 11/12 and joins the mid-ventral body wall at about the middle of 12 and the mid-dorsal

wall at 13/13. The posterior one joins the ventral wall at about the middle of 13 and the dorsal wall at 13/14 and probably is septum 12/13, or possibly 11/12 and 12/13 combined.

The oral end of the alimentary tract is somewhat protruded and has thin walls. In the third and fourth somites the dorsal wall has a heavy mass of glandular and muscular tissue. The esophageal region in 5–7 has relatively thin walls and is followed by two powerful gizzards, one each in 8 and 9 (fig. 2). Posterior to the gizzards the lumen is large and the walls rather thin and highly vascular for the next three or four somites and then the ordinary intestinal character is assumed.

The two gizzards are decidedly more distinct than is indicated in figure 2, which shows them lying in a position oblique to the long axis, and does not well show the marked constriction at the union of the septum 8/9 with the wall of the esophagus, which is shown by sections. The muscular layer is not entirely absent at the constriction, but is reduced in thickness to not over one-eighth of that near the middle of either gizzard.

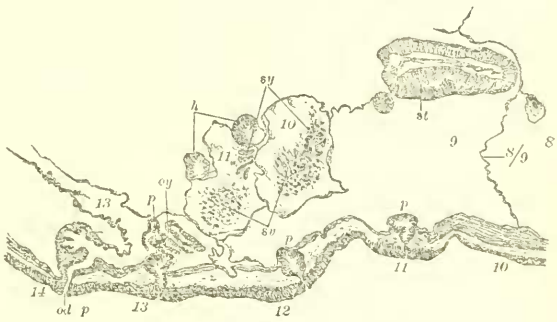

FIG. 3.—SYNGENODRILUS LAMUENSIS. LONGITUDINAL SECTION RECONSTRUCTED FROM SEVERAL SECTIONS PASSING THROUGH THE OVIDUCAL PORE AND THE PROSTATE GLANDS. ×23. *h*, HEART; *od p*, OVIDUCAL PORE; *oy*, OVARY; *p*, PROSTATE GLAND; *st*, SECTION THROUGH SACCULAR PART OF SPERMATHECA; *s v*, SPERM VESICLE; *sy*, SPERMARY; 8, 9, ETC., NUMBERS OF SOMITES.

Definite "hearts" are present in 6 and 7, and four pairs posterior to the septum 7/8 are assumed to belong to somites 8–11 (fig. 3). Organs are assumed to belong to any particular somite to which the hearts with which they are associated are thus assigned.

The worm is meganephric and apparently the first nephridia are in the fourth somite. The nephridia associated with the "hearts" of 8 and 9 seem quite certainly to be connected with the nephridiopores of 8 and 9, although the latter one is far removed from its pore because of the displacement of the septa. Nephridia are present in 10, but the nephridiopores have not been located. They are absent in 11 and 12, present in 13, absent in 14, and present in the following somites.

Two pairs of spermaries and of spermiducal funnels are contained in paired sperm vesicles in 10 and 11, respectively (fig. 3).

The sperm ducts (fig. 4) are slender, much contorted ducts, of which those of one side unite posterior to the septum, which we have assumed may represent the fused septa 9/10, 10/11, and 11/12. From the place of union the combined duct has a fairly direct course to the spermiducal pore on the anterior part of 13. The pores are anterior to the place of union of the septum 12/13 with the body wall. There are no prostatic nor atrial modifications of the sperm ducts, nor any development of papillae in connection with the pores. The presence of abundant sperm cells gives evidence of sexual maturity.

We have found nothing in the literature on Moniligastridae which indicates the presence of sperm sacs in addition to the sperm vesicles, yet such organs are clearly present in the species under discussion. These organs are so interesting in character and the relationships which they suggest are of such importance that a somewhat detailed description is desirable. We use the term sperm vesicles for the chambers which inclose the spermaries and the spermiducal funnels and which are called testikelblasen by Michaelsen (1900:9). We use the term sperm sacs for the storage chambers which are contained in somites adjacent to the testicular somites while communicating with the latter by openings through the intervening septa. Michaelsen calls them samensäcken. The sperm vesicles of either side are in intimate contact and suspended by what is assumed to be a compound septum representing septa 9/10, 10/11, and probably 11/12. The spermaries of either side are borne by the anterior walls of the corresponding sperm vesicles which presumably represent septa 9/10 and 10/11, respectively (fig. 3). Parts of the posterior walls of the sperm vesicles, presumably septa 10/11 and 11/12, have a thickened ciliated epithelium which is much folded and constitutes the spermiducal funnels. Numerous small, thin-walled sacs containing mature sperm cells (fig. 5) project posteriorly from the depressions between these folds and occupy space in the somites 11 and 12, although their cavities communicate with the preceding somites. These sacs

FIG. 4.—SYNGENODRILUS LAMUENSIS. SECTION THROUGH SPERM VESICLES NEAR LATERAL WALLS. ×35. *h*, HEART; *n*, NEPHRIDIUM; *s d*, SPERM DUCT; *s v*, SPERM VESICLES.

have the relations of the sperm sacs (samensäcken) of ordinary earthworms and would correspond fully with these organs if the spermiducal funnels were distinct from the sac-bearing part of the septa, and this part of each septum with its sacs were evaginated into the following somite, thus giving rise to a partially multichambered sac. The contents of these small sacs are almost exclusively sperm cells which are nearly or quite mature.

FIG. 5.—SYNGENODRILUS LAMUENSIS. LONGITUDINAL SECTION RECONSTRUCTED FROM SEVERAL SECTIONS PASSING THROUGH THE SPERMIDUCAL FUNNEL AND RELATED SPERM SACS OF SOMITE 11. ×115. *s c*, SPERM CELLS; *sd f*, SPERMIDUCAL FUNNEL; *s s*, SMALL SPERM SACS; *s v*, SPERM VESICLE.

A pair of extensive sperm sacs communicating with the sperm vesicles, extend dorsally and posteriorly to about the twentieth somite and contain masses of developing sperm cells and are included within the anterior part of corresponding ovisacs (fig. 6). The relations of these sperm sacs are much the same as is found in certain limicoline worms among the Naididae, Tubificidae, and Lumbriculidae. We have here a rather remarkable assemblage of sperm-storing chambers suggesting relationships with various groups of Oligochaeta. The suppression of the sperm vesicles and of the small sacs associated with the spermiducal funnels would give a limicoline condition. The suppression of the pair of dorsal sperm sacs and a somewhat further development of the small sacs of the septal walls would give conditions similar to those in one genus of Lumbricidae, numerous Glossoscolecidae, and in many Megascolecidae. A still further suppression of the sperm vesicles would result in a condition similar to that of many other earthworms, including some of the more primitive Megascolecidae and many Lumbricidae.

FIG. 6.—SYNGENODRILUS LAMUENSIS. LONGITUDINAL SECTION THROUGH THE DORSAL SPERM SAC AND THE OVISAC OF ONE SIDE. ×35. *d s s*, DORSAL SPERM SAC; *o*, OVA; *os*, OVISAC.

In the sections a rather small gland, which is assumed to be a prostate gland, is attached to the ventral body wall at a position slightly laterad of *b* in each of somites 11, 12, and 13 (fig 3). Each gland consists of a tubular glandular part of which the lumen is somewhat contorted and which ends in a very short duct having a length about equal to the combined thickness of the hypodermis and circular muscle layer of the body wall (fig. 7). The lumen of the wider glandular part is bounded by an epithelial layer, associated with a thicker glandular layer which is surrounded by a thin, apparently muscular layer, bounded superficially by a very thin epithelium recognizable only in favorable situations. Presumably these glands are in pairs.

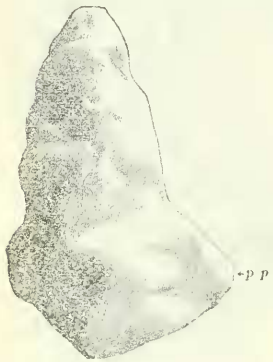

FIG. 7.—SYNGENODRILUS LAMUENSIS. WAX MODEL OF PROSTATE GLAND RECONSTRUCTED FROM SECTIONS, POSTERIOR VIEW. ×75. *p p*, NARROWED PART EXTENDING TO SURFACE OF BODY AT PROSTATE PORE.

The ovaries are rather extensive structures in the anterior part of 13 and the oviducal funnels are wide and lead into very short ducts (fig. 3) which open to the exterior at 13/14, slightly laterad of seta line *b*. The ovisacs have already been mentioned. They inclose the dorsal sperm sacs and extend posteriad of 22 (fig. 6). The ova correspond closely in size and granular contents with those of other Moniligastridae. They are about 0.045 mm. in diameter.

There is a pair of spermathecae in each of somites 8 and 9. Each spermatheca includes a duct and a long tubular sac and there are no spermathecal glands nor atrial chambers such as are found in some of the species of *Moniligaster* and *Drawida*. The spermathecae resemble rather those of the primitive genus *Desmogaster*. The duct of the sectioned spermatheca of 9 is about 1.5 mm. long and but 0.07–0.1 mm. in diameter in the greater part of its length. The septum 8/9 follows the duct rather closely, forming a tubular chamber open toward the posterior (fig. 8). The saccular glandular part is somewhat longer than the duct and about 0.35 mm. in diameter, with a lumen of which the diameter is about one-third as great (fig. 3). A compact mass of spermatozoa extends throughout the greater part of the lumen of

FIG. 8.—SYNGENODRILUS LAMUENSIS. SEMIDIAGRAMMATIC LONGITUDINAL SECTION THROUGH SPERMATHECAL DUCT AND INVESTING SEPTUM, 8/9. ×35. *st d*, SPERMATHECAL DUCT; *st p*, SPERMATHECAL PORE.

the saccular part. The openings to the exterior are in 7/8 and 8/9, slightly ventrad of the seta line *cd*.

Lists of the literature on the Moniligastridae are contained in Michaelsen (1900 and 1909) and Stephenson (1915). The literature is quite extensive but has all been accessible in the preparation of this paper.

The relationships of this species are in part quite clear. It has many of the characters of the Moniligastridae and is most nearly allied to the primitive genus *Desmogaster*. This is obvious from the following definitions of these groups by Michaelsen (1900: 109–110):

MONILIGASTRIDAE.

S-förmig gebogene, einfach-spitzige Hakenborsten, zu 8 an einem Segm., gepaart. Gürtel an $3\frac{1}{n}$ oder 4 Segm., im Bereich der männlichen und weiblichen Poren. Männliche Poren 1 oder 2 Paar, auf Intsegmtf. 10/11 oder 11/12 und 12/13; weibliche Poren 1 Paar, auf Intsegmtf. 11/12 oder vorn am 13. oder 14. Segm.; Samentaschenporen 1 oder 2 Paar, auf Intsegmtf. 7/8 oder 8/9 oder 7/8 und 8/9. Oesophagus mit oder ohne Muskelmagen vor den Hoden-Segm.; 2–10 Muskelmagen am Anfange des Mitteldarms. Letzte Herzen 2 Segm. vor dem Ovarial-Segm. Meganephridisch. Hoden und Samentrichter 1 oder 2 Paar, eingeschlossen in 1 oder 2 Paar Testikelblasen; die Testikelblasen sitzen an dem dissep., das zunächst vor der Intsegmtf. der männlichen Poren inseriert ist; die langen Samenleiter münden in je eine Prostata ein. 1 Paar Ovarien in dem Segm., das zunächst vor der Intsegmtf. bezw. dem Segm. der weiblichen Poren liegt; 1 Paar Eiersäcke ragen von der Hinterwand des Ovarial-Segm. nach hinten. 1 oder 2 Paar Samentaschen mit langem, schlauchförmigem Ausführungsgang.

DESMOGASTER ROSA.

Männliche Poren 2 Paar, auf Intsegmtf. 11/12 und 12/13; weibliche Poren vorn am 14. Segm.; Samentaschenporen 1 oder 2 Paar, auf Intsegmtf. 7/8 oder 8/9 oder 7/8 und 8/9. 7–10 Muskelmagen am Anfange des Mitteldarms. Letzte Herzen im 11. Segm. Meganephridisch. 2 Paar Hoden und Samentrichter, eingeschlossen in 2 Paar Testikelblasen an Dissep. 10/11 und 11/12. Prostaten 2 Paar, lang gestreckt. Ovarien im 13. Segm.; Eiersäcke von Dissep. 13/14 nach hinten ragend. Samentaschen ohne atrium-artige Erweiterung und gestielte Drüsen am distalen Ende des Ausführungsganges.

The chief divergence from *Desmogaster* is in the number and position of the gizzards, and especially in the relations of the sperm ducts and sperm sacs. In the position and number of gizzards the resemblance to the Diplocardiinae is close and the departure from the usual condition in Moniligastridae is considerable. In *Desmogaster* there are two pairs of sperm ducts, which remain independent of each other and each of them enters an atrium (prostate gland), as do the two members of the single pair of sperm ducts of all other previously known members of the family. In the new species, on the contrary, the sperm ducts are entirely independent of the prostate

glands; moreover, the two ducts of either side of the animal unite into one duct, and there is thus but one pair of spermiducal pores, and these are entirely distinct from the prostate gland pores. This is a condition similar to that which is normal in what are considered to be more primitive forms of Megascolecidae, such as some of the Acanthodrilinae and Diplocardiinae, but with one great difference, namely, that in the latter groups the sperm ducts open far posterior (17–19) to the position in which they open in the new form, which is on the anterior part of 13 and presumably anterior to septum 12/13, which is shifted posteriorly, as described above. Considered with reference to internal metamerism, the sperm duct openings correspond in position quite closely with those of *Pelodrilus violaceus* Beddard, in which the two sperm ducts of either side open separately but quite near each other and nearly midway of the length of 12. In most species of *Pelodrilus* the two pairs of spermiducal pores are on adjacent somites.

In the extensive sperm sacs which extend posteriorly from the sperm vesicles and are included in the ovisacs, we have a character in which the new species differs from the earthworms and strongly resembles certain limicoline forms. The unique feature of this sperm sac development is their inclusion within the ovisacs, but perhaps no great stress should be placed on this character, since it does not seem to be found in the Haplotaxidae, from which the earthworm ancestors are assumed to be derived.

Notwithstanding the important differences above mentioned, it seems to us reasonable to include the new species in the family Moniligastridae, at least tentatively, because of the various important characters in which it is allied with *Desmogaster*. This will entail some modification of the definition of that family as will be seen by a comparison of that given at the beginning of the discussion with the one of Michaelsen. It seems to us desirable to recognize a subfamily Syngenodrilinae for the new genus and a subfamily Moniligastrinae for those previously known.

An attempt to arrange *Pelodrilus*, *Syngenodrilus*, *Desmogaster*, and a primitive Acanthodriline form in a phyletic series has met with difficulty because of the peculiar condition in *Desmogaster* in which the sperm ducts of either side are separate and yet open into prostate glands instead of independently of them. If *Desmogaster* is considered as derived from *Syngenodrilus* then we must assume that it was before the union of the sperm ducts in the latter form or else that after such union they again separated and later came into connection with the prostate glands.

The family Haplotaxidae is represented by a considerable number of species of *Pelodrilus* in the South African, Australian, and New Zealand regions. If these regions actually were connected in the

past by such a land area as has been assumed under the name Gondwana, somewhere in that region from Haplotaxid ancestry a Moniligastrid branch may be supposed to have arisen. This branch may have split early into a *Desmogaster* branch which reached and retained a hold in the Burmese and East Indian regions; and a Syngenodriline branch which reached and retained a hold in the tropical East African region. From the latter branch the more primitive Acanthodriline forms may have been derived, and other descendants with but slight change have given rise to our present-day genus *Syngenodrilus*. The suggested relationships are shown in the diagram (fig. 9).

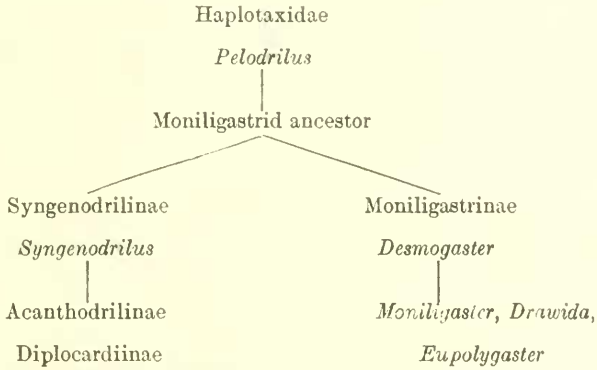

FIG. 9.—DIAGRAM SHOWING SUGGESTED RELATIONS OF SYNGENODRILUS AND RELATED GROUPS.

Because of the lack of adequate knowledge of the earthworm fauna of the territory lying between Northern India and British East Africa, we are, of course, not certain that primitive Moniligastrid forms may not exist in the intervening territory; nor that migration may not have taken place through this territory, or even possibly by the route postulated by Michaelsen (1910: 28), by which the ancestral forms of *Eudichogaster* have been supposed to have passed between Africa and India.

The absence of primitive Moniligastrid species from the Hindustan peninsula and their presence both east and west of that region presents a problem of a sort often encountered in dealing with primitive groups having discontinuous distribution.

The adoption of the ideas of Matthew (1915) on the general principles of geographical distribution will give a very different notion of the sequence of events leading up to the present distribution of earthworms from that held by some writers. These ideas are based on an acceptance of theories of continental development involving the principles of isostasy. They assume a general permanency of the great ocean basins and of the continental shelves. They also assume an alternation of periods of continental elevation, aridity,

and erosion with periods of moist, tropical climate and partial submergence. The great land masses are chiefly in the northern hemisphere and at times of maximum elevation are united into one "irregular land mass with three great projections, South America, Africa, and Australasia, radiating out from it into the southern hemisphere." A lowering from present levels of 600 feet "would isolate North America, South America, Asia, Africa, and Australia as separate insular continents."

One important principle of dispersal as announced by Matthew (1915:180) is as follows: "Whatever agencies may be assigned as the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it."

According to these views we should expect to find the region of origin and the center of dispersal of earthworms to be in the Holarctic region and the more primitive types to be found in the more remote areas as Australia, Africa, and South America; while the more modern, progressive groups are to be expected in Holarctic and adjacent territory. A Gondwana continent would not be needed to account for the present distribution of the Moniligastridae nor an Antarctic continent to explain the distribution of *Notiodrilus* and near relatives and to supply a center of origin and dispersal of earthworms in general, as is sometimes assumed.

Michaelsen (1905:50–55) has expressed views concerning the distribution of the primitive kinds of earthworms which correspond in some ways quite closely with the general principles of distribution enunciated by Matthew.

It seems somewhat surprising that *Syngenodrilus* which seems a very primitive type of earthworm should be found closely associated with such a highly specialized group as *Polytoreutus*, and similarly that *Desmogaster* should be found in a *Pheretima* region.

Family MEGASCOLECIDAE.

Polytoreutus of the subfamily Eudrilinae is a genus which includes about 30 described species, limited in their distribution to a relatively small district in the east-central part of Africa. The two species represented in the Chanler collection involve no change in generic definition.

POLYTOREUTUS CHALONERI, new species.

Length, 10.9 cm. Diameter (maximum), 0.5 cm. Somites, 148. Color (in alcohol), olive buff. Prostomium, prolobic. Setae (pos-

terior to clitellum), *aa: ab: bc: cd*=9:5:8:2; *dd* equals about ½ circumference. Clitellum, 13⅔–⅓18; complete ventrally, 14–½16. Nephridiopores, near seta line *d*. Male pore, median; anterior part of 17. Oviducal pores, posterior part of 14, nearly in line with nephridiopores. Spermathecal pore, median on 18/19. Septa 5/6 and 11/12, somewhat thickened; 6/7–10/11, more strongly thickened. Gizzard in 5. Unpaired esophageal pouches in 9, 10, and 11. Calciferous glands, paired in 13. Sperm vesicles (inclosing spermaries and spermiducal funnels) and sperm magazines in 11. Sperm sacs extend posteriorly from sperm vesicles to about 36. Prostate glands, tubular; open separately into the bursa. Spermatheca, forked at anterior end into two large branches; unpaired median part, without lateral or posterior diverticula.

One specimen, collected at Mkonumbi near Lamu, British East Africa, by William Astor Chanler in 1892.

Holotype.—Cat. No. 16834, U.S.N.M.

Longitudinal sections were made of the half of the anterior 23 somites on the left side of the median sagittal plane. The other half is left united with the remainder of the worm.

External characters.—The olive-buff color of the alcoholic specimen is more pronounced on the dorsal surface than on the ventral. The length of the specimen which is evidently much contracted is 10.9 cm., and the maximum diameter which is at the clitellum is 0.5 cm. There are 148 somites and those anterior to the clitellum are about twice as long as the others and more strongly elevated. The arrangement of the setae in somites posterior to the clitellum is approximately indicated by the formula *aa: ab: bc: cd*=9:5:8:2. *dd* equals about one half the circumference. No evidences of setae were found on 14–16 and only *cd* on 17. The length of seta *b* of somite 9 is 0.25 mm. and of somites just posterior to the clitellum it is about one third greater. No modified genital setae were found. The clitellum includes 14–17 and encroaches slightly on 13 and 18. It is complete ventrally from the anterior border of 14 to the middle of 16 but is incomplete ventrally elsewhere.

The nephridiopores are nearly in seta line *d*, with those of a few anterior somites slightly dorsal to it and others slightly ventrad. The male pore opens mid-ventrally on a small protuberance slightly anterior to the middle of 17. The spermathecal pore is mid-ventral in 18/19. The wall is slightly thickened around each of the two pores but there is no modified genital area. The oviducal pores are on 14, near its posterior border, between seta lines *c* and *d*, but slightly ventrad of the nephridiopores.

Internal characters.—The internal organization of this worm corresponds quite closely with that of other members of the genus. Septa 5/6 and 11/12 are somewhat thickened, while 6/7–10/11 are

more strongly thickened. The large thick-walled gizzard is in 5. The unpaired esophageal pouches in 9, 10, and 11 are ventrad of the alimentary tract and open into it by short, wide ducts (fig. 10). These pouches are ovoid, highly vascular bodies. The paired calciferous glands are in 13 and reniform in shape. Hearts are in 9–11; those of 9 are relatively small and those of 10 and 11 quite large. The spermaries in 11 are included in sperm vesicles which seem to unite across the median line in the anterior ventral part of the somite, between the nerve cord and the ventral vessel. The connecting portion is tubular and of rather small diameter. The spermiducal funnels are included in the sperm vesicles; but the greatly enlarged sperm magazines lie outside (fig. 11), and chiefly laterad and anteriad of them. From the sperm magazines the sperm ducts extend through septum 11/12, and then laterad to the body wall between seta lines *a* and *b*, and then posteriad to the anterior part of 18 where each enters a rather small diverticulum of the corresponding prostate gland.

FIG. 10.—POLYTOREUTUS CHALONERI. SECTION THROUGH ESOPHAGEAL POUCH OF SOMITE 10. ×55. *e*, ESOPHAGUS; *e p*, ESOPHAGEAL POUCH.

The cavities of the sperm sacs are continuous with those of the sperm vesicles (fig. 11, *ss*) and the sacs extend posteriad through a considerable number of somites. They are quite slender as far as the posterior borders of the calciferous glands and the spermathecal furcae

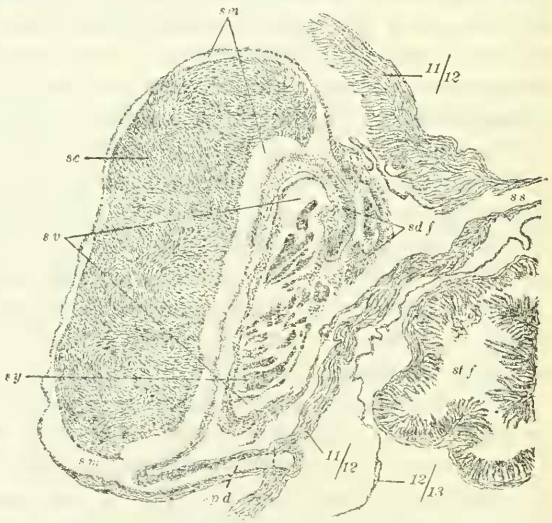

FIG. 11.—POLYTOREUTUS CHALONERI. LONGITUDINAL SECTION RECONSTRUCTED FROM SEVERAL SECTIONS PASSING THROUGH THE SPERM DUCT AND SPERM VESICLE. ×35. *s c*, SPERM CELLS; *sd f*, SPERMIDUCAL FUNNEL; *s m*, SPERM MAGAZINE; *sp d*, SPERM DUCT; *s s*, OPENING INTO SPERM SAC; *st f*, FURCAL BRANCH OF SPERMATHECA; *s v*, SPERM VESICLE (LARGER IN SECTIONS NEARER MIDDLE OF WORM); *sy*, SPERMARY.

(branches), and then are abruptly enlarged and continue as large, more or less irregular bodies, as far as somite 36. Due to the displacement of the calciferous glands and the pushing backwards of the septa, the place of enlargement of the sperm sacs is really about opposite somite 16, as indicated by external metamerism. Each sac has a more or less definite lumen which is accompanied by a branch of the vascular system, at least as far as 23, which is as far as the sections extend.

The prostate glands are each about 10 mm. long and slightly less than 1 mm. in diameter. Each is so bent and folded, that it is included between the septa of 18, although it crowds these outward so as to include most of somites 16-18, as indicated by external metamerism. Near its outlet each gland has a small diverticulum of about 0.5 mm. in length and height, which receives the corresponding sperm duct. The duct of each prostate is quite short, and opens separately into the dorsal part of the cavity of the muscular bursa, which is located medially on the ventral floor of 17, and opens to the exterior slightly anterior to the middle of that somite. The bursa is in height about one-fourth of the diameter of the worm and its lumen is much folded, and presumably during copulation the organ is everted and forms a penis.

The female reproductive organs, in general structure and relations, resemble those of other members of the genus. These relations are indicated to some extent in figure 12 but shown in greater detail in figures 16 and 18 in the species description next following.

Although the female reproductive organs of *Polytoreutus* are more or less similar to those of certain other African genera, to one familiar only with the earthworms of North America, they present somewhat anomalous conditions.

Instead of paired spermathecae with pores anterior to the oviducal pores, we have normally in *Polytoreutus* a more or less fused condition of what was, perhaps, originally a pair of sacs, and also have a single median ventral pore in 18/19 or on 19. The ovarian cells are more commonly found in the ovisacs which are closely related to septum 13/14. There seems to be evidence in support of the view that in some species, at least, these cells are at first related to septum 12/13 and are subsequently shifted to the ovisacs. The oviducts open to the exterior in a normal fashion, but internally each one communicates with the corresponding ovisac and also with the anterior part of the spermathecal apparatus. A further peculiarity of the oviducts of a number of species, is the presence of one or more chambered diverticula, crowded with matured sperm cells and included in a thick-walled enlargement of each oviduct, called by Michaelsen, the eitrichterblase.

In *P. chaloneri* the spermatheca includes a rather large, median sac which branches at the anterior end in 13 into two extensive furcae (fig. 12) and in 17 curves first laterally and dorsally and then ventrally around the bursa and then joins the ventral wall, and communicates with the exterior through the spermathecal pore at the median ventral point of 18/19. The median sac lies ventrad of the nerve cord and between it and the body wall. Each anterior furca or branch curves dorsad and posteriad to a point about midway of the length of the median sac and of the clitellum, but pushes the septa back and so remains in 13, as indicated by the internal metamerism. Each of the pair of oviducts has a rather direct course from the oviducal pore to the enlarged "eitrichterblase" which is attached to the anterior side of 13/14. One sperm-filled diverticulum of the oviduct (samenkämmerchen, Michaelsen) is included in the thick wall of the "eitrichterblase." The remaining part of the oviduct, communicating with the corresponding spermathecal furca near its base, has also a rather direct course.

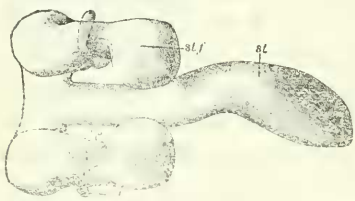

FIG. 12.—POLYTOREUTUS CHALONERI. WAX MODEL RECONSTRUCTED IN PART FROM SECTIONS SHOWING CERTAIN FEMALE REPRODUCTIVE ORGANS. ×7. *od*, OVIDUCT; *os*, OVISAC; *st*, MEDIAN SPERMATHECAL SAC; *st f*, FURCAL BRANCH OF SPERMATHECA.

In *Polytoreutus* the characters of the spermathecae are recognized as of first-class importance for specific distinctions. In a large majority of the 30 or more species already described the spermatheca either lacks anterior furcae or has posterior branches or else the worm has paired copulatory organs near the male pore. Any one of these characters is sufficient to distinguish its possessor from *P. chaloneri.* There are but four species which are not in some such way distinguished from the new form. These four species are *P. baralypton*, *P. finni*, *P. hindei*, and *P. kilindinensis.*

P. baralypton Cognetti (1911) is distinguished from the new form by having the male pore at 17/18 instead of anterior to the middle of 17; by the absence of a muscular bursa associated with the male pore; by the absence of diverticula of the prostate glands at the points of entrance of the sperm ducts; and there are also marked differences between the two species in the number of somites and in the extent of the sperm sacs as well as other minor differences.

P. finni Beddard (1894 and 1901*a*) is distinguished from the new form by its much greater length and tenuity, but especially by having over three times as many somites, over 500, which is a very unusual number. The former species has also much more slender and shorter sperm sacs than has the latter, and the male and spermathecal pores and intervening surface of the former are much

more prominent and conspicuous. A more detailed description of *P. finni* would in all probability reveal still further differences.

P. hindei Beddard (1901*b*) is apparently rather close to the new form. It is sharply distinguished by the presence of a strongly developed sucker-like area on the ventral wall of 17 and 18, which includes the male and spermathecal apertures. The sperm sacs of the former species are extremely slender and much shorter than in the latter; the sperm ducts enter the narrow parts of the prostates close to the bursa instead of entering diverticula of the enlarged glandular parts as in the new species; and, finally, the median sac of the former becomes much diminished in size posteriorly, and the furcal branches extend much further posteriorly than in the new form.

P. kilindinensis Beddard (1894 and 1901*a*) differs from the new species in some respects. The male pore is on 17/18 in the former instead of being anterior to the middle of 17, as in the new form; there is a prominent modified genital area on 18 to 21 in the former and none in the latter; there is absence of any "samenkämmerchen" in the former; and the median spermathecal sac is very slender in the former with the spermathecal pore on the middle of 19, while in the new species the median sac is much larger and the spermathecal pore is on 18/19.

POLYTOREUTUS MULTIPORUS, new species.

Length, 10–20.5 cm. Diameter (maximum), 0.3–0.5½ cm. Somites, 264–485. Color (in alcohol), pale gray-brown. Prostomium, prolobic. Setae (posterior to clitellum), $aa:ab:bc:cd=4:2:5:\frac{5}{6}$; *dd* equals about one-half of the circumference. Ventral setae of 19–26 or 27, modified and on papillae. Clitellum, 14–17 and encroaching on 13 and 18. Nephridiopores, between seta lines *c* and *d*. Male pore, median; posterior part of 17. Oviducal pores, posterior part of 14; in seta line *c*. Spermathecal pore, median on 18/19. Accessory spermathecal pores, median on 19/20–24/25 or 25/26. Septa 5/6 and 11/12, somewhat thickened; and 6/7–10/11, more strongly thickened. Gizzard in 5. Unpaired esophageal pouches in 9, 10, and 11. Calciferous glands, paired in 13. "Hearts," large in 10 and 11; smaller in 9. Spermaries and spermiducal funnels, inclosed in sperm vesicles in 11. Sperm sacs extend from sperm vesicles in 11 through many somites. Prostate glands open separately into an eversible muscular bursa and extend posteriorly through a number of somites. Sperm ducts enter prostates not far from their connection with the bursa. Oviducts and ovisacs have the relations usually found in the genus; the former with one or two "samenkämmerchen." Spermatheca, forked at anterior end into two large branches which are connected with the oviducts; unpaired median sac without diverticula

extends to spermathecal pore; a median spermathecal branch with several pairs of lateral diverticula extends posteriad from near the pore through about seven somites and has median ventral intersegmental pores on 19/20–24/25 or 25/26.

Five specimens collected at Mkonumbi near Lamu, British East Africa, by William Astor Chanler in 1892.

Holotype and paratypes.—Cat. No. 16835, U.S.N.M.

The paratype from which the drawing was made for figure 13 is left unsectioned. Sagittal sections were made from one-half of the first 20 anterior somites of the type-specimen and similar sections from a varying number of anterior somites in three paratypes. In each instance the uncut half was left connected with the remainder of the specimen.

This treatment of type-specimens is not a common one among students of earthworms, but seems to us to scarcely need defense, since it permits the careful detailed study of the internal organs

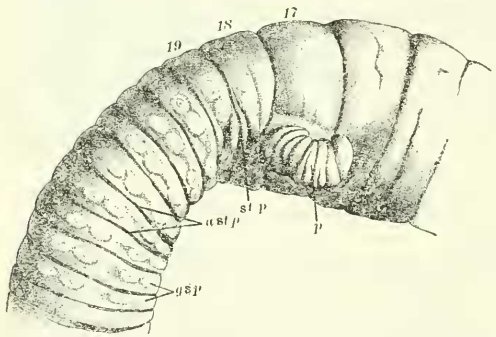

FIG. 13.—POLYTOREUTUS MULTIPORUS. VENTRAL VIEW OF GENITAL REGION. ×5. *a st p*, ACCESSORY SPERMATHECAL PORES; *g s p*, MODIFIED SETAE AND PAPILLAE; *p*, PENIS; *st p*, SPERMATHECAL PORE.

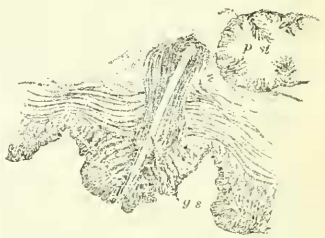

FIG. 14.—POLYTOREUTUS MULTIPORUS. LONGITUDINAL SECTION SHOWING MODIFIED SETA (*a* OF 19). ×35. *g s*, MODIFIED SETA; *p st*, DIVERTICULUM OF POSTERIOR BRANCH OF SPERMATHECA.

which is so essential for adequate descriptions in this group of animals. It also avoids the disturbance and occasional loss of organs which sometimes accompanies exploratory dissections.

External characters.—The length of the type-specimen is 14.5 cm., and its maximum diameter is 0.45 cm. There are about 470 somites in the type and 485 in the largest paratype of which the length is 20.5 cm. The shorter specimens have fewer somites and may not be complete. The color of the specimens indicates that they were pigmented on the antero-dorsal surface in life. The setae are absent on five or six anterior somites and in the clitellar region. Each of all or nearly all of the ventral setae on 19–26 or 27 is surrounded by a glandular papilla (fig. 13) and is modified, being nearly straight (fig. 14) and of fully twice the length and nearly twice the diameter of the ordinary setae which are quite small (fig. 15). Throughout the greater part of the length of the worm the setal distances are about as indicated by the formula given above. The clitellum is

much less strongly developed on the ventral side of the somites than elsewhere. It includes 14–17 and encroaches slightly on 13 and 18.

Dorsal pores are lacking. The nephridiopores are rather conspicuous near the intersegmental grooves and between the seta lines *c* and *d*. The male pore is conspicuous on the posterior part of 17, and in one paratype there is a protruding penis (fig. 13), which is directed anteriorly and has a length of about one-half of the diameter of the body. The oviducal pores are near the posterior border of 14, in the seta line *c*, and are rather inconspicuous. The spermathecal pore is a median transverse cleft on 18/19. Inconspicuous, median, intersegmental pores are present on 19/20–24/25 or 25/26 and open into a posterior extension of the spermatheca (fig. 16).

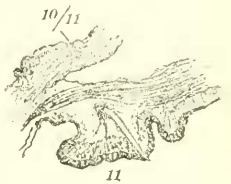

FIG. 15.—POLYTOREUTUS MULTIPORUS. ORDINARY SETA. (*a* OF 11). ×35.

Internal characters.—The thickened septa of the anterior somites correspond in position and thickness with those described in most species of the genus. There is nothing peculiar in the alimentary tract, which has a powerful gizzard in 5, unpaired ventral pouches in 9, 10, and 11, and a pair of calciferous glands in 13. Careful attention to the septal relations is necessary, or one is in danger of locating these glands in 15, since they are pushed back with the septum 13/14 past the incomplete septum 14/15. This dislocation is due to the presence of the massive anterior branches of the spermatheca, which nearly fill the space normally belonging to 13. The alimentary tract abruptly widens to form the intestine, slightly posterior to the opening of the calciferous glands into the esophagus. The "hearts" in 10 and 11 are very large, those of 9 are considerably smaller, and there appears to be a still more slender pair of vessels connecting the dorsal and ventral vessels in 8; but the vascular system anterior to 9 has not been carefully studied, and no positive statement can be made concerning a possible doubling of the dorsal vessel in anterior somites.

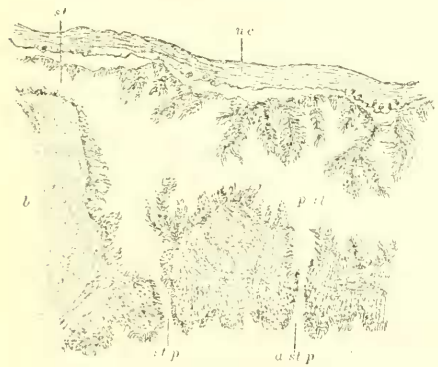

FIG. 16.—POLYTOREUTUS MULTIPORUS. LONGITUDINAL SECTION SHOWING THE SPERMATHECA NEAR THE SPERMATHECAL PORE. ×35. *a st p*, MOST ANTERIOR ACCESSORY SPERMATHECAL PORE AT 19/20; *b*, EDGE OF BURSA; *n c*, NERVE CORD; *st*, POSTERIOR PART OF MEDIAN SPERMATHECAL SAC (THROUGH NARROW EDGE); *p st*, POSTERIOR BRANCH OF SPERMATHECA; *st p*, SPERMATHECAL PORE AT 18/19.

Paired sperm vesicles in 11 include the spermaries, the spermiducal funnels, but not the sperm magazines. From the sperm vesicles the

two sperm sacs extend posteriorly as narrow tubes through a considerable number of somites to points near the posterior ends of the prostate glands, and are then enlarged and crowded with sperm masses. In the type-specimen the enlarged parts of the sperm sac extend from about 40 to 80, and in a paratype from 40 to 64. From the ventro-anterior part of each magazine the corresponding sperm duct extends posteriorly along the body wall to the region of the corresponding prostate gland where it turns dorsally and follows the course of the gland for a short distance and then enters it through a small knoblike diverticulum. Each gland is long, tubular, and somewhat contorted. Its diameter is less for a short distance near the opening of the gland into the enlarged muscular bursa. Traced from the bursa the glands curve dorsally, one on either side of the intestine, make an abrupt turn at the points of entrance of the sperm ducts, and extend posteriad, parallel with the long axis of the worm and dorsad of the intestine. In the type-specimen they end in 40, and in one paratype in 38. In another paratype one extends to 28 and the other to 35.

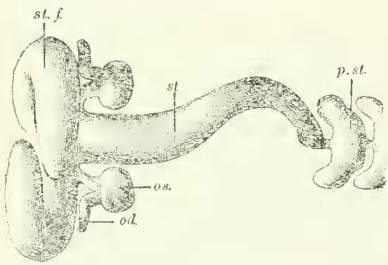

FIG. 17.—POLYTOREUTUS MULTIPORUS. WAX MODEL RECONSTRUCTED IN PART FROM SECTIONS SHOWING CERTAIN FEMALE REPRODUCTIVE ORGANS. ×10. *od*, OVIDUCT; *os*, OVISAC; *p st*, PART OF POSTERIOR BRANCH OF SPERMATHECA; *st*, MEDIAN SPERMATHECAL SAC; *st f*, FURCAL BRANCH OF SPERMATHECA.

The spermatheca is an unpaired tubular organ located ventrad of the alimentary canal, and the median part is ventrad of the nerve cord. The spermatheca forks at the anterior end into right and left branches (fig. 17, *st f*), which are large and encircle the alimentary tract. In one paratype the free ends extend beyond the mid-dorsal line. The diameter of the median part of the spermatheca is distinctly less than that of the proximal parts of the branches. The spermatheca extends posteriorly from the bifurcation along the mid-ventral line close to the body wall until it reaches the bursa around which it curves to the left or right and opens to the exterior mid-ventrally on 18/19.

The wall of the median sac becomes gradually thinner in the part adjacent to the bursa and is quite thin near the pore. Posterior to the pore there is an extension of the spermatheca (fig. 17, *p st*) which has a rather narrow median part in close contact with the body wall and extends posteriad to 25 or 26. Paired diverticula metamerically disposed communicate with the median sac opposite the intersegmental pores in 19/20–24/25 or 25/26 through which the median sac opens to the exterior. The wall of this posterior extension of the spermatheca (fig. 16, *p st*) is identical in structure with that of the spermatheca just anterior to the spermathecal pore in 18/19. The

diverticula are free from the body wall and extend laterally to about seta line *b*. The pores are referred to in the definition and in the description of figures as accessory spermathecal pores (fig. 16, *a st p*).

From the oviducal pores on the posterior part of 14, each of the oviducts extends ventrad and then in a quite direct course to the enlargement (eitrichterblase) just anteriad of the corresponding ovisac (figs. 17 and 18B). From this it is continued in a rather direct course to the corresponding furcal branch of the spermatheca with which it communicates. One or two "samenkämmerchen" open into each duct and are more commonly compound with three or four diverticula opening through a common ductule into the oviduct. Figure 18B, *sk* is from a section through the single compound chamber of this kind in the type specimen, and is through the cavities of three such diverticula, all of which communicate with the oviduct through a common opening.

The pocketlike chambers of the ovisacs, besides well-grown ova, contain ovarian cells in various growth stages (fig. 18, A and B). No evidence was found throwing light on the place of origin of the ovarian tissue.

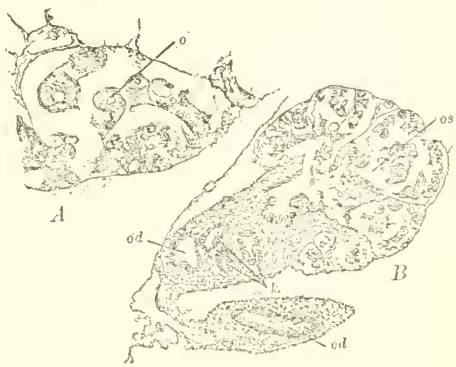

FIG. 18.—POLYTOREUTUS MULTIPORUS. SECTION THROUGH OVISAC. A. ×350. *o*, OVARIAN CELLS IN DIFFERENT GROWTH STAGES. B. ×55. *od*, OVIDUCT; *os*, OVISAC; *sk*, DIVERTICULA OF THE MULTICHAMBERED SAMENKÄMMERCHEN.

It is apparent from the description of the new species that it belongs to the genus *Polytoreutus*. *P. multiporus* differs from all other described species of the genus in the following respects: There are accessory spermathecal pores at 19/20–24/25 or 25/26 which open from the posterior extension of the spermatheca; the ventral setae of 19–26 or 27 are much modified and surrounded by papillae. The above characters sharply distinguish the new species from others thus far known. By the two large branches of the spermatheca at its anterior end, *P. multiporus* is related to a group which includes *P. chaloneri* and its allied forms, discussed in an earlier part of the paper, but is sufficiently distinguished from any of them by the above-mentioned characters.

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